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RUNNING HEAD: Hand distance modulates tactile selective attention

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Abstract

This study investigated whether the N140cc ERP component, described as a possible electrophysiological marker of target selection in touch, was modulated by body posture. Participants performed a tactile search task in which they had to localise a tactile target, presented to the left or right hand, while a simultaneous distractor was delivered to the opposite hand. Importantly, the distance between target and distractor (hands separation) was manipulated in different experimental conditions (near vs. far hands). Results showed reduced errors and enhanced amplitudes of the late N140cc when the hands were far apart than in close proximity. This suggests that the competition between target and distractor is stronger when the hands are close together in the near condition, resulting in a degraded selection process. These findings confirm that the N140cc reflects target selection during the simultaneous presentation of competing stimuli and demonstrate for the first time that the attentional mechanisms indexed by this ERP component are based at least in part on postural representations of the body.

Keywords: touch, selective attention, event-related potentials, body posture, body representation,

1. Introduction

One fundamental function of selective attention is to resolve the competition between the stimuli that constantly reach our sensory organs. Stimuli that are relevant for our behaviour have to be selected while irrelevant information is filtered out (Desimone & Duncan, 1995). In the experimental setting, such competition between stimuli is typically investigated in tasks using multi-stimuli arrays in which a task-relevant target is simultaneously presented with one or more irrelevant distractors. Participants are instructed to ignore the distractors and to respond to the presence or one feature of the target. When competitive stimuli are presented with the target, error rates and reaction times tend to increase. This is particularly evident when the target can be distinguished from the distractors on the basis of a conjunction of features as opposed to a unique feature (Treisman & Gelade, 1980).

While selective attention has been widely studied in the visual domain, the mechanisms underlying the attentional selection of the target in touch remains largely unexplored. Only a handful of studies to date have investigated the situation in which a competing tactile stimulus is presented in conjunction with the tactile target. Results have typically shown that the presence of a distractor lowers accuracy and increases response times (e.g. Driver & Grossenbacher, 1996; Evans & Craig, 1991; Evans, Craig & Rinker, 1992; Marcel et al., 2004). More specifically, performance is impaired on incongruent trials when target and distractor differ (with respect to a specific feature such as stimulus duration, stimulus pattern or motion direction for moving stimuli, etc.) as compared to congruent trials when

they are identical. The resulting distractor-interference effect (the difference between congruent and incongruent trials) has been considered an index of efficiency; that is, how well participants can focus attention on the relevant target locations while ignoring the irrelevant stimuli.

One relevant question concerns the effects of the spatial separation between the target and the distractor in tactile search tasks. In vision, the interference effect reduces as the distance between the target and the distractor increases (e.g. Eriksen & Eriksen, 1974; Moray, 1969). While this general principle appears to work also for tactile stimuli, with stronger distractor-interference observed when the distractor is presented closer to the target (Craig, 1974; Soto-Faraco, Ronald & Spence, 2004), this effect seems to be further modulated by the specific location of the stimuli over the body. Importantly, the distance between tactile stimuli can be encoded according to multiple reference frames. The somatotopic distance between stimuli is exclusively determined by the spatial separation between the mechanoreceptors of the skin activated by the tactile stimuli, and is independent of body posture. However, because the body can assume a number of different postures, the same tactile distance can also be encoded according to an external reference frame based on external space, which requires the integration of proprioceptive and visual cues relative to the body position in space with tactile information. While changes between the distance of the target and the distractors will often correspond to changes in both the somatotopic and the external spatial representations of these stimuli, it is possible to selectively increase/decrease the somatotopic distance between stimuli in the absence of any changes to the external distance and vice-

versa. Therefore, the manipulation of the distance between the target and the distractor in touch can provide a relevant insight into the reference frames upon which tactile attention operates.

Using moving stimuli, Evans and Craig (1991) found significant distractor interference effects when the target and the distractor were presented to different fingers of the same hand. However, this interference effect was not observed when the stimuli were presented to fingers of different hands (Evans & Craig, 1991). Because the external distance between fingers was kept constant in the two tasks (stimuli on the same or on different hands), these results were interpreted as evidence supporting a somatotopic representation of spatial attention (see also Evans et al., 1992, for similar results), with maximal interference effects when the stimuli were somatotopically close. In a separate study in which the stimuli were presented to different hands but the body posture was manipulated (the two hands were placed close together or far apart), Evans and colleagues (1992) showed the presence of a small interference effect which was not modulated by hand posture with both stationary and moving stimuli. Because the external, but not the somatotopic distance changed during the postural manipulation, these findings appear to provide additional evidence that tactile selectivity operate exclusively according to a somatotopic reference frame.

However, a different pattern of results was observed in later studies using a similar paradigm. When participants were instructed to focus their attention on one hand in order to report a nonspatial feature of the tactile target (long vs. short stimulus) while ignoring a simultaneous tactile distractor to the other hand (which

could be identical or different from the target), the distractor-interference effect was reduced when the hands were positioned far apart than close together (Driver & Grossenbacher, 1996). Because this postural manipulation did not change the somatotopic separation between tactile stimuli (stimuli were always presented to the same portion of skin), these findings suggest that, at least under certain circumstances, tactile selectivity operates according to an external spatial reference frame. More recently, Soto-Faraco et al. (2004) showed the presence of a distractor-interference effect when participants had to determine the elevation of a tactile target that could be presented to one of four possible locations (top and bottom locations, i.e. index and thumb of the left or right hand) while a distractor was simultaneously presented to one of the three remaining locations. Responses were slower and less accurate when target and distractor were presented at different elevations (one top and the other bottom and vice-versa; incongruent condition) than at the same elevation (congruent condition). Importantly, the distance between the hands modulated the distractor interference, with a larger distractor effect being observed when the hands were in close proximity rather than spread apart.

Thus, while some studies suggest that tactile selectivity operates according to a purely somatotopic reference frame, others point to the presence of a higher-order external frame of reference[1]. While many different factors could have contributed to these differences (for example, differences between the target-distractor distance in the far condition across studies), it is interesting to note that stimulus duration and response times were considerably shorter in studies suggesting a somatotopic spatial representation as compared to those supporting an external reference frame.

Evidence has shown that tactile stimuli are initially encoded according to a somatotopic representation of the body (independent of body posture) but are later recoded or remapped onto an external representation of space which is based on the integration of tactile with proprioceptive and visual information about the body (e.g. Azañón & Soto-Faraco, 2008; Longo, Azañón & Haggard, 2010; Röder, Rösler & Spence, 2004; Shore, Gray, Spry & Spence, 2005). Because tactile remapping is a dynamic and constructive process mediated by different sensory and cognitive factors (see Badde & Heed, 2016, for a recent review), tactile selectivity might operate according to different reference frames depending on the remapping phase that characterises the processing stages upon which it operates (e.g. Spence & Gallace, 2007).

The aim of the present study was to investigate whether the behavioural and neural correlates of target selection during a tactile search task are modulated by body posture. More specifically, we studied whether the manipulation of the distance between tactile target and distractor in external space affected the operations of tactile selectivity. To investigate the unfolding of neural processes over time, event-related potentials (ERPs) were recorded during a tactile selective attention task in which participants were asked to localise a target (single tap) presented to the right or left index finger while ignoring a simultaneous distractor (double tap) presented to the index finger of the opposite hand. In different experimental conditions, participants performed the same tactile task with their index fingers placed in close proximity without touching (near condition) or far apart (far condition).

We focused on the N140cc ERP component, identified in a previous study as a possible electrophysiological marker of target selection in touch (Forster, Tziraki & Jones, 2016). This lateralized component is characterized by an enhanced negativity at central electrodes over the hemisphere contralateral to the target side as compared to the ipsilateral hemisphere. The N140cc was observed between 140 and 340 ms poststimulus onset overlapping with the N140 somatosensory component as well as the later N2 component. Importantly, in Forster and colleagues' study (2016) participants had to determine the presence or absence of a tactile target presented amongst distractors when these stimuli were presented to different fingers of the two hands ('hand task') and when they were delivered to different body parts ('body task': the two hands, shoulders and feet). The amplitude of the N140cc was larger in the hand task than in the body task. Because the distance between the target and the distractors was reduced in the hand task as compared to the body task, this finding might suggest increased attentional resources when the competition between stimuli is increased. However, this hypothesis was ruled out by an additional data analysis in which only trials where the target was presented to the same hand location were included (i.e. only the distractor body location varied between the hand and the body tasks) showing no N140cc amplitude difference between tasks. Based on these results, Forster et al. (2016) concluded that the stronger N140cc components observed in the hand task as compared to the body task were due to differences between the spatial acuity of the body sites stimulated in the two tasks, with enhanced lateralized components where spatial acuity is maximal (i.e. when stimuli are presented to the hands) and in

line with studies in the visual domain (e.g. Schaffer, Schubö & Meinecke, 2011). Although these findings suggest that the attentional mechanisms involved in target selection operate according to a somatotopic frame of reference, it is not possible to completely rule out a role of the external reference frame, because the target-distractor distance varied according to both spatial frames in the hand and body tasks.

In the present study, changes in the distance between the hands did not vary the somatotopic distance between the target and the distractor (presented to the index fingers of the left and right hand), but only affected their distance in external space. If the allocation of tactile attention is based exclusively on a somatotopic representation, no differences should emerge between the amplitude or the time course of the N140cc in the different experimental conditions. On the contrary, if tactile selective attention operates upon an external postural representation of the body, we expect to observe systematic differences between the N140cc elicited under the near and far hands conditions.

2. Method

2.1 Participants

Nineteen young adults were recruited via the University's employment website and took part in the present study. Three participants were excluded from the analysis due to a low number of trials after artefact rejection (less than 50% of the trials for at least one of the experimental conditions). Thus, the final sample was composed of sixteen participants (10 females; 20-30 years-old age range - mean age

24.6 years). Fifteen participants were right-handed and all of them had normal or corrected-to-normal vision and no history of major neurological diseases. This project was approved by the University of Edinburgh's Psychology Research Ethics Committee and followed the Helsinki Declaration principles. All participants signed an informed consent prior to start the experiment and were compensated for their participation (£7.5 per hour).

2.2 Stimuli, apparatus and procedure

Participants were tested in a sound-attenuated cabin, resting their hands on a table. The distance between participants' hands was manipulated, so that their index fingers were placed in close contiguity (2 cm) without touching (near condition), or they were spaced apart at a distance of 70 cm (far condition). A fixation point was secured to the table between participants' hands. It was equally distant from the left and right index fingers and was aligned with their body midline. To mask the sounds made by tactile stimulators, one speaker was positioned on the table close to the hands and presented white noise (65 dB SPL) throughout the experimental blocks. Tactile stimuli were presented using 12 V solenoids (Heijo Research Electronics, UK) driving a metal rod with a blunt conical tip. The tip of the tactile stimulators touched the skin whenever a current passed through the solenoid. Two solenoids were attached with adhesive medical tape to the inner side of the top phalanx of the left and right index fingers. Participants responded using two pedals vertically arranged and positioned under the same foot (top and bottom pedals).

Each trial started with a 500 ms empty interval, which was followed by the simultaneous presentation of the tactile target to one hand and of the distractor to the other hand (300 ms duration). Targets consisted of a single tap during which the rod made contact with the skin for 300 ms. Distractors were double taps (two 75 ms stimulations separated by a 150 ms interval). Stimulus presentation was followed by a 1500 ms interval, which was used to collect foot responses.

Each participant completed eight blocks of 100 trials. In each block, tactile targets were presented randomly and with equal probability to the left or right hand. Therefore, on 50 trials the target was delivered to the left hand requiring a top pedal response, while on the remaining 50 trials it was presented to the right hand requiring a bottom pedal response.

Participants' task was to identify whether the tactile target was presented to the left or right index finger by pressing the top or bottom pedal with the toes or heel of the same foot, respectively. They were instructed to keep their eyes on the central fixation at all times and to press the pedals as fast and as accurately as possible.

Participants completed four blocks with the hands in the near position and four blocks with the hand in the far position. The order of these conditions was counterbalanced across participants so that half of the participants started with the hands in the near position, while the other half started with the hands in the far position. Hand posture was changed after four consecutive blocks for half of the participants. For the remaining participants, hand posture was changed every two blocks. To avoid ERP contamination from motor responses, the responding foot

operating the top and bottom pedals was changed after the first two blocks and then again before the last two blocks, so that overall participants completed four blocks with their left foot and four with their right foot (the starting foot – left vs. right – was counterbalanced across participants).

Prior to the beginning of the experiment, participants completed two practice blocks of 50 trials each (which were repeated whenever average accuracy fell below 60% during this training). At the end of each block participants received verbal feedback about their performance (average response time and accuracy).

2.3 Recording and data analysis

EEG was recorded from 70 active electrodes (Biosemi ActiveTwo system; 512 Hz sampling rate; 40 Hz upper cut-off frequency with a high-pass filter of 0.53 Hz and a notch filter of 50 Hz). Eye movements were monitored by bipolar horizontal and vertical EOG derivations. EEG was digitally re-referenced to the average of the left and right earlobes and epoched into 600 ms periods, starting 100 ms before cue onset. Trials with eye blinks (VEOG exceeding ± 60 μV), horizontal eye movements (HEOG exceeding ± 40 μV) or other artefacts (a voltage exceeding ± 80 μV at any other electrode) were excluded from the analysis. Overall, 92% of the trials were included in the ERP analyses after artefacts rejection. ERPs to tactile stimuli on correct trials (73% of the trials) were averaged for all combinations of hand distance (near vs. far), target position (left vs. right) and hemisphere (left vs. right).

Mean amplitude values were computed at electrodes C5/6 (where the lateralized components of interest were maximal in the present study, see Figure 2),

within two 80 ms latency windows (140-220 ms and 230-310 ms). To investigate whether hand distance modulated the electrophysiological signature of attentional tactile target selection (N140cc), repeated measures Analyses of Variance (ANOVAs) were carried out for the factors hand distance (near vs. far), target side (left vs. right) and laterality (hemisphere contralateral vs. ipsilateral to the target side). In these analyses, the presence of reliable lateralized components is reflected by the main effect of the factor laterality, indicating significant differences between the hemisphere contralateral and ipsilateral to the target side.

For the behavioural analyses, mean reaction times (RTs) for correct responses obtained in the 200-1500 ms interval, as well as choice error rates, were submitted to separate repeated measures ANOVAs with hand distance (near vs. far) and target side (left vs. right) as within subjects factors.

For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were applied where appropriate. Unless specifically stated otherwise, nonsignificant results are not reported.

3. Results

3.1 Behavioral Results

Omission errors were observed on 5.4% of trials and were excluded from further analyses. The repeated measures ANOVA conducted on choice error rates showed a main effect of hand distance, $F_{1,15} = 7.7$, $p = 0.01$, partial $\eta^2 = .34$, with participants' performance showing a higher error rate in the near ($M = .16$, $SD = .10$) than far condition ($M = .12$, $SD = .06$). No significant main effect of target side nor an interaction between target side and hand distance were observed (both $F_{1,15} < 3$, p

>.10). The repeated measures ANOVA on RTs did not show any significant main effects or interactions (all $F < 1.2$, all $p > .3$).

3.2 ERP results

Figure 1 (left panel) shows ERP waveforms elicited at electrodes C5/6 contralateral (solid lines) and ipsilateral (dashed lines) to the location of the tactile target, separately for the hands far and hands near conditions (top and bottom panels, respectively). The corresponding difference waveforms (Figure 1, right panel) were obtained by subtracting ERPs elicited at electrodes ipsilateral to the target from contralateral ERPs. The scalp distribution of the lateralized components observed in the hands far and hands near conditions in the 140-220 ms and 230-310 ms intervals are shown in Figure 2.

********** INSERT FIGURE1 ABOUT HERE**********

********** INSERT FIGURE2 ABOUT HERE**********

In line with existing evidence (Forster et al., 2016), ERPs elicited over the hemisphere contralateral to target were more negative as compared to those measured over the ipsilateral hemisphere. In the present study, these lateralizations were characterized by two distinct phases. The early phase of the enhanced negativity contralateral to the target emerged in the N140 time window (140-220 ms), while the late phase of this lateralized component overlapped with the N2 component (230 - 310 ms). In both hands near and hands far conditions, enhanced

negativities contralateral to the target side were present in both the early and late time windows considered, but these lateralizations appeared to be stronger when the hands were far apart.

Statistical analyses revealed the presence of a reliable N140cc (main effect of the factor laterality, $F_{1,15}$ = 26.1, p < .001, partial η^2 = .63) between 140 and 220 ms poststimulus onset. A significant N140cc was observed in both the hands far and hands near conditions ($F_{1,15}$ = 12.7, p =.003, partial η^2 = .46 and $F_{1,15}$ = 6.3, p = .024, partial η^2 = .29, respectively). However, despite the fact that mean N140cc amplitude values in this interval were larger for hands far than for hands near (M = .37 μV, SEM = .1 μV vs. M = .2 μV, SEM = .08 μV, respectively), this difference was not significant ($F_{1,15}$ = 1.37, p = .26, partial η^2 = .08).

Between 230 and 310 ms poststimulus onset, the main effect of the factor laterality ($F_{1,15}$ = 31.8, p < .001, partial η^2 = .68) demonstrated systematic differences between ERPs contralateral and ipsilateral to the target side, demonstrating the presence of the late phase of the N140cc component. Importantly, the late N140cc was modulated by hand distance (Laterality x Hand Distance, $F_{1,15}$ = 4.7, p = .047, partial η^2 = .24). Follow-up analyses conducted separately for each condition revealed the presence of significant lateralizations in the hands far (M = .8 μV, SEM =.14 μV, $F_{1,15}$ = 30.3, p < .001, partial η^2 = .67) as well as in the hands near (M = .48 μV, SEM = .12 μV, $F_{1,15}$ = 15, p < .001, partial η^2 = .5) conditions. Thus, the N140cc component was present in both hand posture conditions, but its amplitude was reliably larger when the hands were far apart than close together as shown by the Laterality x Hand Distance interaction.

4. Discussion

In the present study we investigated whether the electrophysiological correlates of target selectivity in touch varied as a function of the distance between the tactile target and distractor. Tactile stimuli were presented to the index fingers of the left and right hand, and participants performed the same tactile search task with their hands close together (2 cm) or far apart (70 cm). Thus, the external distance between the target and the tactile distractor was varied while the somatotopic distance between stimuli was held constant.

The crucial finding of the present study was that the external distance between target and distractors affected the operations of tactile selective attention as revealed by both the behavioural and the electrophysiological results. The analysis of participants' responses showed that accuracy was reduced in the near hand condition, when target and distractor were close together, as compared to when the hands were far apart. No difference was observed in the speed of responses in the two hand positions. This pattern of results (effect of hand distance on accuracy but not response speed) is in line with previous behavioural studies, which used a similar task as the present one in which the target location was spatially uncertain (Soto-Faraco et al., 2004, Exp. 4). The fact that participants were systematically less accurate when the hands were close together demonstrates that the separation of target and distractor in external space influenced tactile selectivity.

ERPs results showed that the hemisphere contralateral to the target was more negative as compared to the ipsilateral one. The presence of this enhanced

negativity, which was maximal at electrodes close to the somatosensory cortex, is in line with existing electrophysiological evidence observed in a tactile search task (Forster et al., 2016). Despite relevant methodological differences, the presence of centrally distributed lateralized components in both the present and Forster et al.'s studies (2016) provides further evidence that these lateralizations can index the neural processes underlying target selection in a tactile search task. However, there were also relevant differences between the lateralized ERP components elicited in the present study and those observed in Forster and colleagues' study (2016). First, the *onset* of these lateralizations differed between studies with earlier lateralized ERP components observed here as compared to Forster et al. (2016). In the present study, the discrimination between target and distractors could only start 75 ms poststimulus (after the onset of the distractor gap). This means that there is a temporal dissociation between nonlateralized ERP components time-locked to the search array onset and the lateralized components, which were time-locked to the distractor gap. Thus, in the present study, lateralizations starting around 140 ms poststimulus onset are in fact occurring about 70 ms after the gap onset. The fact that reliable lateralizations appeared earlier in the present study as compared to the study of Forster and colleagues (2016) could be explained by the different number of items presented in the search arrays (two and six, respectively), with fewer items resulting in faster target identification and earlier lateralized components. A second difference between studies involves the *time course* of the enhanced negativity contralateral to the target side. As shown in Figure 1, the lateralizations observed in the present study are characterized by two distinct phases, an early one overlapping

with the somatosensory N140 component and a later one overlapping with the N2 component. By contrast, in Forster et al.'s study (2016) ERP lateralizations started about 140 ms and remained present until approximately 340 ms poststimulus onset. The specific pattern of lateralizations observed here are likely due to the stimuli chosen as target and distractors and to the fact that these were not counterbalanced across participants. During the gap that characterized the distractor, only one finger was tactually stimulated (where the target was presented). It is therefore possible that no lateralized components were elicited during this interval of unilateral tactile stimulation. If this specific pattern of lateralizations is driven primarily by the physical properties of the stimuli, then the early and late lateralized components observed in the present study are likely to reflect the same cognitive processes. Accordingly, we called these lateralizations early and late N140cc, in line with existing ERP evidence (Forster et al., 2016).

While the onset and time course of the N140cc observed in the present study are worth discussing given the limited number of ERP studies on tactile selectivity in search tasks, the aim of this study was to assess the impact of body posture on this lateralized component. We found systematic differences between the N140cc components measured in the near and far conditions. More specifically, the amplitudes of the late N140cc components were reduced when the hands were close together than far apart; that is, when the selection of the target was more difficult. Thus, both behavioural and electrophysiological measures confirmed that tactile selective attention is modulated by the hand separation in external space. This suggests that the mechanisms of tactile selective attention operate after visual

and proprioceptive information about body posture (or target-distractor distance) are integrated with tactile information. Consequently, these findings show the impact of an external reference frame on tactile selectivity at least under certain experimental circumstances, providing additional evidence for the hypothesis that multiple reference frames might contribute to the selection of relevant information in touch. In fact, it is possible that the contribution of each of these reference frames is not fixed, but flexibly changes over time depending on the specific task requirements.

Indeed, previous studies have shown that tactile stimuli are initially encoded according to a somatotopic representation of the body, which is independent of body posture (e.g. Kaas, 1983; Overvliet, Anema, Brenner, Dijkerman & Smeets, 2011; Röder et al., 2004). However, starting from approximately 130 ms poststimulus, tactile information is recoded from a somatotopic onto an external representation of space, which takes into account the position of the body (e.g. Azañón & Soto-Faraco, 2008; Longo et al., 2010; Röder et al., 2004; Rigato, Ali, van Velzen & Bremner, 2014). One interesting observation is that in the present study this difference between hand postures was observed in the later but not in the early phase of the N140cc component. As discussed earlier, the late phase of the N140cc emerged approximately 150 ms after the onset of the gap in the distractor (i.e. 75 ms after the search array onset). Consistent with existing literature (e.g. Azañón & Soto-Faraco, 2008; Longo et al., 2010; Röder et al., 2004; Rigato et al., 2014), this observation suggests that the effect of body posture on tactile selectivity becomes evident only after the onset of tactile remapping. Taken together, the results of the

present study demonstrate the impact of an external reference frame on tactile selectivity. This conclusion might appear in contrast with existing ERP evidence suggesting that target selection indexed by the N140cc is primarily based on a somatotopic reference frame (Forster et al., 2016). However, the different tasks used in these studies might explain these differences. Although it has been suggested that remapping of touch from somatotopic to external coordinates is an automatic process, no remapping appears to take place when the selection/discrimination of the target does not explicitly involve a spatial dimension. More specifically, responses to tactile stimuli are not affected by manipulations of body posture (crossed vs. uncrossed hands) when participants have to discriminate a nonspatial feature of the tactile stimuli (Medina, McCloskey, Coslett & Rapp, 2014; Ruzzoli & Soto-Faraco, 2017). Because participants had to report the presence or absence of the target in Forster et al.'s study (2016), it is possible that tactile stimuli were not remapped onto external space during this nonspatial task.

In the present study, proprioceptive information was manipulated through changes in body posture (hands near vs. far). Importantly, however, the hands were visible throughout the task; therefore, both proprioceptive and visual information might have contributed to the differences observed between the near and far conditions. Previous behavioural studies have demonstrated that both proprioceptive as well as visual information can mediate the hand separation effect on attention. For example, comparable modulations of the distractor-interference effect were observed when participants viewed their hands as well as when they

were blindfolded (Driver & Grossenbacher, 1996), suggesting that the effect of hand posture was primarily mediated by proprioceptive signals. However, effects of hand separation were also found when proprioceptive cues about the body position were held constant while the visual separation between the hands was manipulated using a mirror (Soto-Faraco et al., 2004). This 'virtual' hand separation effect resulted in larger interference effects on accuracy when the hands appeared close together than far apart, suggesting that visual information alone might also suffice to induce a hand separation effect. Thus, both proprioceptive and visual information might independently contribute to the effect of hand separation on tactile selectivity. Future studies should systematically investigate the differences between the effects of hands separation on the electrophysiological correlates of selective tactile attention when visual cues are manipulated but proprioceptive cues are held constant and vice-versa.

Converging evidence that tactile attention is modulated by hand position come from existing ERP studies investigating spatial attention in touch (Eimer, Forster, Fieger & Harbich, 2004; Gillmeister, Adler & Forster, 2010; Pang & Müller, 2017). More specifically, when participants were instructed to focus their attention to one of their hands in order to respond to tactile targets presented at that location, effects of attention on touch were stronger (Eimer et al., 2004) and started earlier (Gillmeister et al., 2010) when the hands were far apart than close together. Interestingly, in both these studies the effects of proprioception on spatial attention occurred within a similar timeframe as the one observed in the present study. These findings were interpreted as evidence that the operations of tactile spatial attention

are more efficient when the distance between the attended and unattended tactile stimuli is increased in external space, even if their somatotopic distance remains unchanged. Despite the fact that distinct neural mechanisms are likely to be responsible for the attentional selection of the cued stimulus location (when this location is known before stimulus presentation; spatial cuing studies of attention) and for the attentional selection of a tactile target presented amongst distractors (when its location not known in advance; tactile search tasks), these converging evidence seems to suggest that different operations of attention are consistently modulated by multisensory information about the position of the body in external space.

To our knowledge, this is only the second study tracking the correlates of tactile target selection over time in a tactile search task[2]. Although little is known about the functional significance of the N140cc component, it has been suggested that it might be the tactile equivalent of the N2pc component observed in visual search tasks (e.g. Forster et al., 2016). This component, which is considered the electrophysiological correlate of visual target selection, is an enhanced negativity contralateral to the target that is typically elicited over posterior electrodes (P07/8) between 200-300 ms poststimulus when the visual target is presented amongst distractors (e.g. Eimer, 1996; Luck & Hillyard, 1994). While it is necessary to be cautious in making such parallels between lateralized ERP components given the substantial differences between the visual and the somatosensory systems, the N2pc has been widely used to investigate the allocation of selective attention during a search task (see Eimer, 2014, and Woodman, 2013, for recent reviews). Therefore, it

might be relevant to consider existing evidence related to the distance between target and distractor in visual search tasks in relation to our findings.

Recent ERP studies using a visual search distractor paradigm have shown smaller N2pc amplitudes (and increased error rates) when the spatial proximity between the salient target singleton and the salient but irrelevant distractor singleton was reduced (Hilimire, Mounts, Parks & Corballis, 2009; 2010). This evidence was interpreted as supporting a degraded selection process due to increased competition between the stimuli (Hilimire et al., 2009; 2010). While other studies have failed to observe any N2pc modulations when the distance between the irrelevant distractors and the target was manipulated (Mazza, Turatto & Caramazza, 2009), these findings were observed during efficient search tasks in which the target was quickly identified (e.g. pop-out tasks). Hence, it is possible that the saliency and/or the similarity between stimuli are relevant factors mediating the target-distractor distance effect, with N2pc amplitude modulations by distance only present in search tasks characterized by strong competition between the target and a salient distractor (e.g. Hilimire et al., 2009; 2010). In the present study, target and distractor were both salient and similar (their difference could only be perceived as time unfolded). Accordingly, the finding that the amplitude of the late N140cc is reduced when target and distractor are closer might reflect increased mutual suppression between relevant and irrelevant stimuli in the near condition in line with ERP evidence from inefficient visual search distractor tasks (e.g. Hilimire et al., 2009; 2010).

This hypothesis should be fully investigated in future studies in which the neural processes linked to target selection and distractor suppression are independently investigated. Studies in the visual domain have shown that there might be two temporally overlapping sub-components of the N2pc: a negativity contralateral to the target which reflects attentional enhancement of target processing (target selection) and a positivity contralateral to the distractor associated with distractor suppression/inhibition (e.g. Hickey, Di Lollo & McDonald 2009; Hilimire & Corballis, 2014; Sawaki & Luck, 2010). In the present study, on each trial one target and one distractor were presented to opposite hands, which are represented by opposite hemispheres in the brain. Thus, in principle, both the selection of the target (contralateral negativity) and the suppression of the distractor (contralateral positivity) might have boosted the lateralization observed, especially if these processes were temporally overlapping. It is therefore crucial to establish whether, analogously to the visual modality, the electrophysiological correlates of distractor suppression can be dissociated from the neural mechanisms of target selection in touch.

In summary, the study presented here demonstrates for the first time that the amplitude of the N140cc – considered the electrophysiological marker of target selection in touch – is modulated by the distance between target and distractor in external space (hands separation effect) during the simultaneous presentation of these competing stimuli. Our findings suggest that when target and distractor are close together, the competition between these stimuli increases, resulting in degraded target selection processes as revealed by higher error rates and reduced

amplitudes of the late N140cc in the hands near condition, in line with evidence from the visual domain (Hilimire et al., 2009; 2010). These findings reveal that tactile selectivity, indexed by the N140cc, operates not only according to a somatotopic frame of reference (Forster et al., 2016) but also according to external and postural reference frames, providing additional evidence that tactile attention is sensitive to the multisensory input coming from other sensory modalities.

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Footnotes:

[1] Another relevant difference across studies concerns the fact that the target location was specified in advance (e.g. Evans & Craig, 1991; Evans et al., 1992; Driver & Grossenbacher, 1996; Marcel et al., 2004). While this might have engaged tactile spatial attention in addition to tactile selective attention, it has been shown that the interference effect is present when the target appears at a predictable location as well as at an unpredictable location (Soto-Faraco et al., 2004). The fact that an effect of body posture on tactile selectivity was observed when the target location was (Driver & Grossenbahcer, 1996) and was not known in advance (Soto-Faraco et al., 2004), rules out the possibility that this experimental manipulation is the sole factor behind the differences observed.

[2] A recent ERP study investigating tactile working memory (Katus, Grubert & Eimer, 2015) has described a central negativity contralateral to the array of tactile stimuli that had to be encoded and maintained in working memory. This enhanced negativity was characterized by an early and a late phase which were considered to reflect the spatially selective encoding and maintenance of task-relevant information (analogously to the N2pc and CDA observed in the visual domain). However, the task used in these studies differs considerably from the classic search task in which one target has to be identified amongst distractors and its location is unpredictable (in Katus and colleagues' study, 2015, all stimuli on one side were to be attended/encoded and the relevant side was known in advance). Thus, it remains to be established whether the early lateralizations observed by Katus et al. (2015) reflect the attentional mechanisms underlying target selection.

Figure captions:

Figure 1. Grand-averaged ERPs elicited by the tactile stimuli in the 400-msec interval after search array onset at central electrodes C5/6 contralateral (dashed lines) and ipsilateral (solid lines) to the hand where the target was presented are shown separately for the Hands Far (top) and Hands Near (bottom) conditions. The N140cc component is shown in the difference waveforms on the right, which were obtained by subtracting ipsilateral from contralateral ERPs for the Hands Far (solid line) and Hands Near (dashed line) conditions.

Figure 2. The topographic maps (top view) show the scalp distribution of the N140cc component for the two analysis intervals (140-220 ms and 230–310 ms) after search array onset for the Hands Far (top) and Hands Near (bottom) conditions. Maps were constructed by spherical spline interpolation (Perrin, Pernier, Bertrand & Echallier, 1989) after mirroring the ipsilateral–contralateral difference waveforms to obtain symmetrical voltage values for both hemispheres.

Figure1

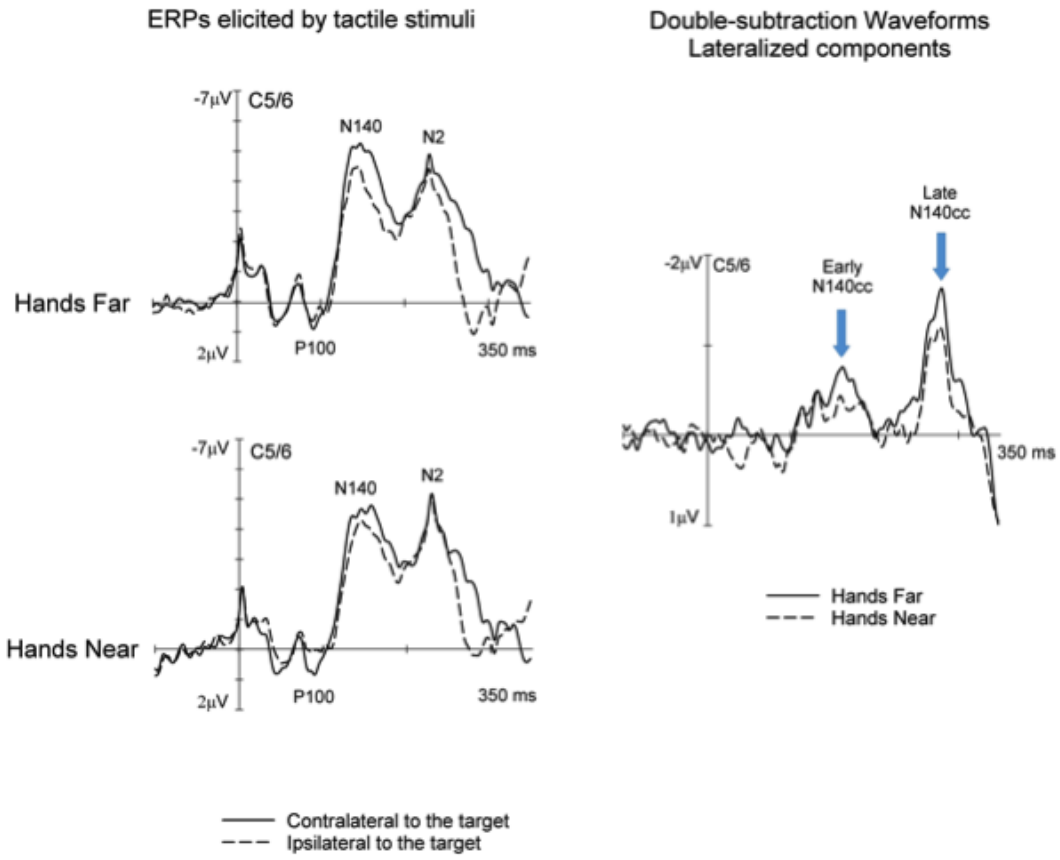
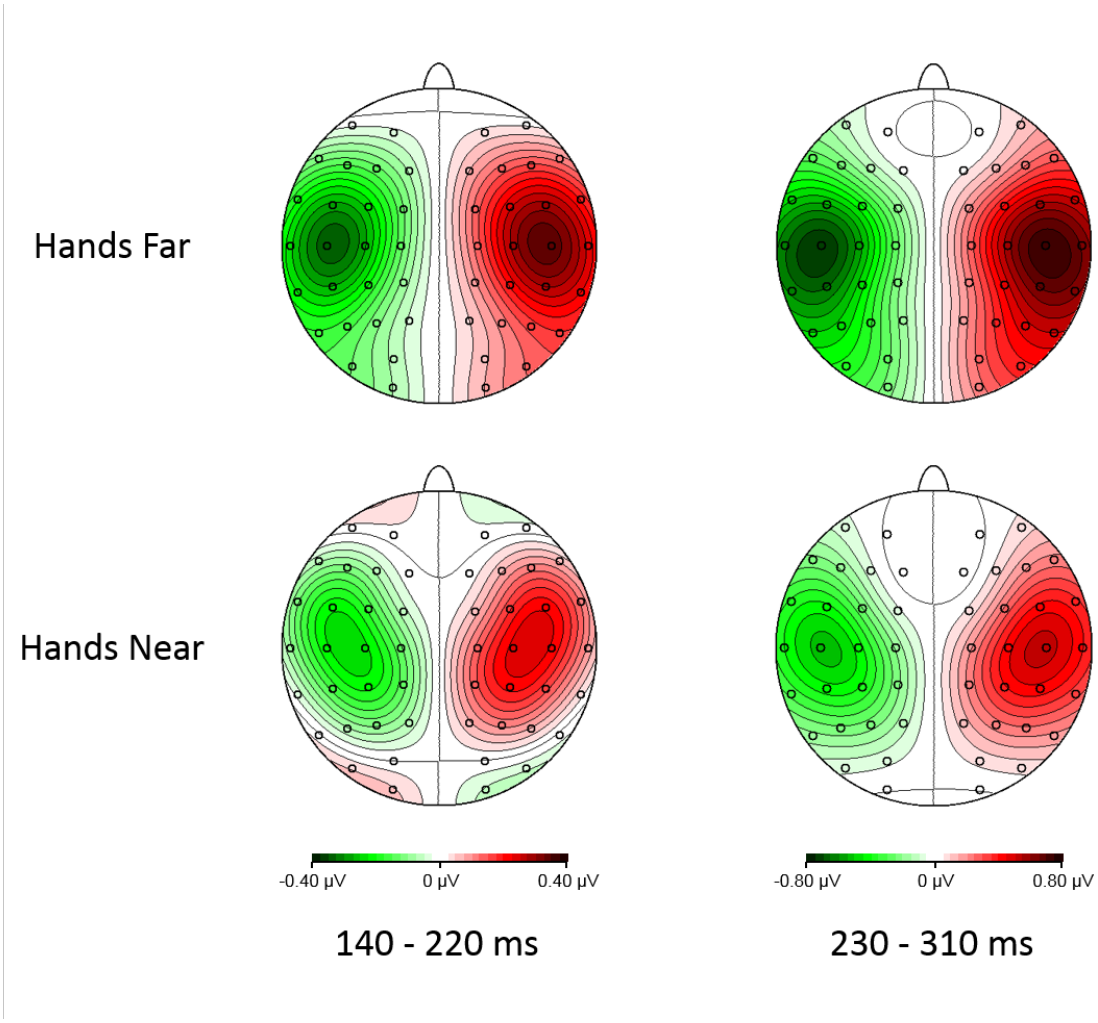

ERPs elicited by tactile stimuli
-7μV
C5/6
N140
N2
Hands Far
2μV
P100
350 ms
-7μV
C5/6
N140
N2
Hands Near
2μV
P100
350 ms
Contralateral to the target
Ipsilateral to the target
Double-subtraction Waveforms
Lateralized components
Late
N140cc
-2μV
C5/6
Early
N140cc
1μV
350 ms
Hands Far
Hands Near

Figure 2


Hands Far
Hands Near
-0.40 µV
0 µV
0.40 µV
-0.80 µV
0 µV
0.80 µV
140 - 220 ms
230 - 310 ms